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Acoustic coordination by allied male dolphins in a cooperative context

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Abstract

Synchronous displays are hallmarks of many animal societies, ranging from the pulsing flashes of fireflies, to military marching in humans. Such displays are known to facilitate mate attraction or signal relationship quality. Across many taxa, synchronous male displays appear to be driven by competition, while synchronous displays in humans are thought to be unique in that they serve a cooperative function. Indeed, it is well established that human synchrony promotes cooperative endeavours and increases success in joint action tasks. We examine another system in which synchrony is tightly linked to cooperative behaviour. Male bottlenose dolphins form long-lasting, multi-level, cooperative alliances in which they engage in coordinated efforts to coerce single oestrus females. Previous work has revealed the importance of motor synchrony in dolphin alliance behaviour. Here, we demonstrate that allied dolphins also engage in acoustic coordination whereby males will actively match the tempo and, in some cases, synchronise the production of their threat vocalisation when coercing females. This finding demonstrates that male dolphins are capable of acoustic coordination in a cooperative context and, moreover, suggests that both motor and acoustic coordination are features of coalitionary behaviour that are not limited to humans.

Introduction

Behaviours that involve ritualised movement or the coordination or synchronisation of signals can be found in a diverse array of taxa. Synchronous movements among individuals are ubiquitous in human societies, with examples including dancing and marching in unison [1]. In non-human animals, well-known examples of synchronous visual signals include claw waving in male fiddler crabs [2], and the flashing of male fireflies [3,4], both of which function in mate attraction. The coordination of acoustic signals also plays a key role in mate attraction in both insects and anurans [5]. For example, male katydids precisely synchronise their acoustic signals in the presence of females [6]. In all these cases, synchrony is defined as the precise coincidence of events in time [7], with such precise synchrony shown to be competitive rather than cooperative, as signallers are vying to be the leading male in order to attract the female [2,6].

Interestingly, while competition appears to drive many synchronous animal displays [8,9], the proximate and ultimate causes of human synchrony are strongly linked to cooperation. Over the years, extensive experimental work has revealed the important role that human synchrony plays in promoting in-group bonding [10–12], fostering cooperation [13–15] and diminishing the perceived formidability of competitors [10]. Furthermore, humans that engage in synchronous behaviour may have increased success in subsequent joint action tasks, whereby coordinated action sharpens the perceptual and motor skills required to participate in collaborative endeavours [14]. As such, the relationship between social bonding and coordinated behaviour in humans is well established, with both physical and verbal synchrony promoting affiliation and enhancing cooperative effort [16].

There are, however, many other forms of temporal coordination with regards to signal production [17]. These include duetting, defined as coupled, simultaneous and/or alternating

chorusing, which does not necessarily involve synchrony [17]. Duetting is found in anurans [5], gibbons [18], lemurs [19] and numerous birds [20], in fact, some species are capable of such precise temporal alternation during duets that it sounds as if only one individual is singing [20,21]. In most cases, duets occur between mated pairs and appear to facilitate the cooperative defence of shared resources [18,22], promote pair bonding [18,19,23], or advertise relationship quality [24]. Turn-taking is a similar form of acoustic coordination that has received much interest in recent years, with individuals timing their vocal output to avoid overlap during exchanges. Humans [25], meerkats [26] and marmosets [27] all engage in turn-taking, for example. Coordinated behaviours can, therefore, take a number of forms with varying temporal characteristics.

Here, we examine another system in which motor synchrony is tightly linked to cooperative behaviour. In Shark Bay, Western Australia, male Indo-Pacific bottlenose dolphins [28] form long-lasting, cooperative alliances [29], which engage in coordinated efforts to compete with rival alliances over access to females [29,30]. The core unit of male social organisation is the 'second-order alliance', typically comprised of 4-14 males. Within these second-order alliances, pairs or trios of allied males, known as 'first-order alliances', work together to herd single oestrus females during events termed 'consortships' [29]. Multiple first-order alliances from the same second-order alliance may participate in attempts to steal females from competing alliances, or defend against such attempts [29]. These strong alliance relationships can last for decades and are critical to each male's reproductive success [29]. This is because males cannot monopolise and defend females on their own due to the intense competition for receptive females, minimal sexual size dimorphism, and because the three-dimensional habitat impedes coerced mating by single males [29].

Motor synchrony has been shown to play an important role in promoting cooperation between these allied dolphins, purportedly acting as a signal of alliance unity [31–33]. First-order allies will surface side-by-side synchronously, usually less than a meter apart, and break the surface within 80–120 ms of each other [32]. The males frequently perform elaborate and synchronous physical displays in the female's presence [32,34]. These displays include a variety of synchronous underwater and aerial leaps and turns. Furthermore, synchrony between second-order allies is most common during bouts of social behaviour with female consorts [32].

During consortships, males use female-directed aggression to constrain her movement and keep her away from competing males [29]. To facilitate this, males produce threat vocalisations called ‘pops’, which are narrow-band, low frequency (1-2 kHz), pulsed vocalisations that are produced in repetitive trains [35]. Pop trains are produced almost exclusively during consortships, and function as an agonistic ‘come-hither’ demand that induces the female to remain close to the popping male [35,36] and may facilitate guard-switching between males [37]. Pops are, therefore, a largely coercive signal with a strong association with physical threats [35]. While pop trains were thought to be produced primarily by individual males, recent observations of multiple males apparently coordinating their pop production required investigation.

In this study, we investigated whether allied male dolphins engaged in acoustic coordination when cooperating in the herding of single females, as a means of furthering our understanding of the evolutionary importance of cooperative, coordinated behaviour in promoting collective action across non-human taxa. Given the prevalence of physical synchrony in this cooperative context, we hypothesised that males might also engage in acoustic synchrony. With our long-term (>30 years) dataset on the association histories of

well-known individuals as a basis, we used a combination of contemporary behavioural observations, acoustic recordings and individual animal localisation to (*i*) assess whether males coordinated pop production in cooperative contexts, and (*ii*) determine the extent to which acoustic coordination occurred among allied males across the population.

Methods

Our long-term dolphin research has been run on a seasonal basis (typically austral winter-spring) off Monkey Mia in the eastern gulf of Shark Bay since 1982, and off Useless Loop in the western gulf of Shark Bay since 2007. Detailed association, behavioural and ranging data have been collected since the mid-1980s in the eastern gulf, and as part of systematic sampling in the western gulf study area since its inception. We use survey data to estimate the proportion of time spent together by different individuals. A "survey" is defined by a minimum five-min observation of dolphin group composition and behaviour, where "group" is defined using the 10 m 'chain rule' (where all individuals were considered part of the same group if they were within 10 m of any other individual [38]). This data is used to calculate association indices using the Simple Ratio Index, which is an estimate of the proportion of time two animals spend together (0 for pairs of animals that never associate; 1 for pairs always seen together). Male alliances are defined both by their association indices (> 0.2 for second-order alliance partners) and their functional behaviour, e.g. cooperating in the herding and defence of females [38–40].

Data collection

Data for this study on male alliance behaviour were collected in the months of Jun-Nov from 2016 to 2018 in Shark Bay's eastern gulf, and May-Sep in 2016 and 2018 in the western gulf. Behavioural and acoustic data were collected from a small (<7m) research vessel, from which we towed an array consisting of four HTI-96 MIN series hydrophones (flat frequency response: 0.002–30 kHz +/- 1 dB) as per King et al. [39]. Recordings were made onto a TASCAM DR-680 MKII multi-track recorder at a sampling rate of 96 kHz. A spoken track that was synchronised with the acoustic recording was used to note the bearing (compass bearing, where the vessel's bow was 0°), distance (m) and identification of the focal animals

at each surfacing. Voice notes were also used to describe notable behaviours (i.e. physical synchrony, displays, aggression) performed by alliance members.

During observations of focal groups of adult males (i.e., first-order alliances), the engine was switched off whenever possible to maximise the signal-to-noise ratio of the recordings. Acoustic data were collected during both focal follows and opportunistic recordings. During each focal follow, the following variables were verified every five mins: group composition, predominant group behavioural state and predominant group spread. All occurrences of changes to group composition or important behavioural events were also recorded during the focal follows. During opportunistic recordings, continuous sampling was used to record any behavioural changes. Focal follows and opportunistic recordings lasted between 60 and 300 minutes. Behavioural state definitions and consortship criteria from the Shark Bay Dolphin Research Ethogram are provided in the ESM.

Acoustic analysis

Acoustic recordings were analysed by inspecting spectrograms (FFT length 1024, Hamming window) in Adobe Audition CC (v. 10.0.2). Pops were visually identified and graded as either individual pop trains or multi-male pop trains. The former represented the predominant type of pop train recorded, where pops are produced in a stereotyped sequence, and the latter represented cases of rapid popping with irregular timing of pop intervals. To characterize variation in the temporal properties of individual and multi-male pop trains, we manually measured the time between consecutive pops within a train, termed the 'inter-pop interval' (IPIs); and the time between consecutive pop trains, termed the 'inter-train interval' (ITIs). ITIs were at least twice the length of the preceding IPI, and typically featured a short tonal component at approximately 5 kHz. Consecutive pop trains were grouped into sequences. Sequence boundaries were defined by acoustic assessment, where the assessor could hear the

vocalising animal cease pop production for a period of time notably longer than the preceding ITIs for that sequence of trains, and where there was no terminal tonal component.

Acoustic localisation

Localisation was used to determine the spatial and temporal arrangement of consecutive pops in both individual and multi-male pop trains. Acoustic localisation was performed using the MATLAB based TOADY program [41]. Localisation error of the array was calculated using custom-written MATLAB routines to calculate 2D averaged MINNA (minimum number of receiver array) localisations using the methods described in Wahlberg et al. [42] and Schulz et al. [43]. The array was calibrated using two different pop trains previously recorded from this population. Acoustic localisation errors for pop directions (n = 50) were calculated as 100% within ± 15° of the true location, 94% within ± 10°, and 68% within ± 5°. However, variation in estimated direction within a train was low, with < 2° difference between sequential pops in a train produced by an individual male. Only vocalisations with a high signal-to-noise ratio were used for localisation. If pops in multi-male trains were partly overlapped, only the non-overlapping portions were localised, and the bearing compared to the preceding and subsequent pops in the train.

Statistical analysis

All statistical procedures were conducted in R 3.4.4 (R project for statistical computing; GNU project). To determine whether the distribution of IPIs differed between individual and multi-male pop trains, we built a linear mixed-effects model (lme using nlme package in R) with IPI as our response variable. The model predictor was pop train type as a nominal variable (individual or multi-male) with second-order alliance membership included as a random effect. To account for the violation of the homoscedasticity assumption, we explicitly modelled the differences in variance between pop train type using the 'varIdent' function

196 (nlme package in R). The full model was compared to a null model containing only the
197 random effect. Model selection was performed by ranking them using log-likelihood (logLik)
198 and Akaike's Information Criterion (AIC). Visual assessment of the residuals confirmed that
199 they were normally distributed. To check for model stability, we used the 'influence' function
200 (car package in R) to assess the influence of each grouping level of the random effect
201 (second-order alliance). The model selection table is provided in the ESM.
202
203 To assess whether males modified temporal characteristics of pops during multi-male trains,
204 we first characterised individual pop trains across our entire dataset. We calculated the slope
205 of the regression line for each individual pop train to determine whether there was tendency
206 for IPIs to increase or decrease over the duration of the pop train. To explore within and
207 between individual variation in more detail we assessed smooth linear change in IPI over the
208 duration of the pop train for six individual males from four different second-order alliances.
209 We then used Pearson product moment correlation to test whether males (i.e., male A and
210 male B) synchronised their pop tempo (IPI) when producing pops in multi-male trains. To
211 test whether this correlation was higher than expected by chance, a null model was
212 constructed by randomly pairing male A's pop train with a randomly selected pop train
213 produced by another male, matched for number of pops. This procedure was repeated 1,000
214 times to generate 1,000 null correlation coefficients from randomly permuted datasets. The
215 true correlation coefficient was then compared to this null distribution to determine whether it
216 was higher than expected by chance (alpha level = 0.05), which would indicate that the males
217 attempt to match their partners tempo when producing pops in multi-male trains.
218
219 Next, to test whether the males coordinated their pop train production by starting and
220 stopping their pop trains at the same time, we calculated the total overlap of male A and male
221 B's pop trains in a multi-male sequence. This was calculated by using acoustic localisation to

222 determine the start and end of each male's pop train, and calculating the percentage of time
223 over a multi-male pop train sequence where the pop trains overlapped. For each multi-male
224 pop train sequence, we took 1 s either side of the sequence as our start and end point for the
225 time shift analysis. However, if another vocalisation type occurred shortly before or after the
226 pop train sequence, we then took the time between the pop train starting/ending and the
227 vocalisation. Thus, the minimum time between the multi-male pop train sequence and the
228 start or end point for the time shift analysis was 250 ms and the maximum was 1 s. This
229 meant the time shift analysis was concentrated over the multi-pop train sequence. As such, a
230 high percentage overlap is expected to occur by chance levels. The null model was
231 constructed by performing the time shift analysis where the pop trains of one male were
232 shifted by a given interval relative to the pop trains of the other male. We linked the start and
233 end of the entire sequence and shifted the sequences relative to one another by a randomly
234 selected time shift (a distribution ranging from 100 ms to the maximum length of the
235 sequence in 100 ms increments), resulting in a different set of overlaps, and a different
236 computed overlap rate (similar to [26]). An overlap probability distribution from 1,000 time
237 shift randomisations was generated and compared to the observed value.

Results

Acoustic data were analysed from 13 focal group follows of 7 different second-order alliances (comprising a total of 59 males), with a total recording time of 22 h and 5 mins from the austral springs of 2016-2018. All recordings were made during consortships and featured both pop trains produced by individual males (Fig. 1A), and instances of possible coordinated pop production (referred to as 'multi-male' hereafter, Fig. 1B).

A total of 6,082 inter-pop intervals from 453 pop trains were measured: 2,415 intervals from trains produced by individual males (281 trains), and 3,667 from multi-male trains (172 trains). A summary of individual male and multi-male pop train characteristics are provided in Table 1. Multi-male pop trains were, on average, longer with more pops per train and shorter inter-pop intervals. This is because in multi-male trains, two males rapidly alternate pop production, so we were measuring the inter-pop intervals between consecutive pops i.e., between two different males. Comparison of the interval distributions between individual male and multi-male pop trains confirmed that they clearly differed (linear mixed-effects model: estimate = -0.048, CI: -0.051 to -0.046; $P < 0.0001$; Figure S1).

Table 1. Summary of individual male and multi-male pop train characteristics. Mean and range of number of pops per train, inter-pop interval and pop train length.

	Individual male pop trains	Multi-male pop trains
Mean number of pops per train	9.6 (range: 2 – 49)	22.3 (range: 3 – 194)
Mean inter-pop interval between consecutive pops (s)	0.115 (range: 0.016 – 0.377)	0.064 (range: 0.0006 – 0.372)
Mean pop train length (s)	0.96 (range: 0.21 – 5.84)	1.70 (range: 0.19 – 25.5)

Individual identification

Localisation of a subset of pops returned consistent bearings for consecutive pops in trains produced by individual males (95 pops, 16 trains across five second-order alliances).

Consecutive pops within the same train differed on average by 0.2° (SD = 1.93°, min = 0.00°, max 6.55°). Figure S2 illustrates two examples of individual male pop trains produced by males from different second-order alliances with associated bearing information. Whilst the bearings change over the course of the pop trains, they do so in a predictable way, either steadily increasing to infer the individuals' movement in a constant direction (Fig. S2A), or with small variation around one bearing, inferring the animal remained stationary whilst vocalising (Fig. S2B). In contrast, multi-male pop trains returned two dominant bearings, which alternated with consecutive pops (244 pops across five second-order alliances). Bearings between consecutive pops varied by 4.43° on average (SD = 3.94°, min = 0.08°, max 17.46°), however, bearing differences between every second pop were comparable to those measured for individual male trains, varying by 0.23° on average (SD = 1.96°, min = 0.00°, max 16.84°). Despite not always being able to identify which two of the three allied males were engaging in this behaviour (due to their proximity), the consistent difference in bearings between consecutive pops in multi-male trains confirmed that the pops were being produced by two different males. Figure 2 illustrates two examples of multi-male trains from different second-order alliances, with bearing information demonstrating the alternation of pops achieved by two different males. Additional examples of localised multi-male pop trains are provided in the ESM (Fig. S2C&D).

Tempo adjustment

There is no consistent systematic change in IPI over time in single male pop trains (Fig. 3). Individuals may increase or decrease the IPI in any given train as shown by the distribution of positive and negative slopes (Fig. 3A). This is further supported by Figure 3B, where the variability both within and between individuals is apparent. The pop trains presented were produced in a five-minute time period for each male (different recordings for all males except SMO + COO), with males producing trains that both increase and decrease in IPI.

We used acoustic localisation to explore the temporal patterning of each male's pops, when they called as part of a multi-male pop train, in more detail. Interestingly, inter-pop intervals were highly correlated between males when they coordinated pop production in these multi-male trains (Pearson correlation: $r_{95} = 0.91$, $P < 0.0001$). Figure 4 shows the distribution of localised pop intervals for two males in multi-male pop trains (i.e., the inter-pop interval for pops produced by male A and the inter-pop interval for pops produced by male B) with corresponding Pearson correlation coefficients. Four of five male dyads from different second-order alliances significantly correlated their tempo, even as the tempo changed over the duration of the pop trains (Fig. 4A). Permutations revealed that the correlation coefficients for all four pairs were significantly stronger than expected if the males were modulating their tempo independently of one another (Fig. 4B). We should note that for the fifth pair (AC alliance; Fig. 4), only one extended pop train was used for this analysis (4 - 10 pop trains were included for the other four alliances; Fig. 4). However, even though they did not show a correlation in tempo, they did appear to maintain a constant tempo with little variation between individuals (i.e. male A range = +/-0.01 sec, male B range = +/-0.03 sec, difference between male A and male B range = +/- 0.01 sec).

Pop train co-occurrence

We present three cases of male dyads from three different second-order alliances where males coordinated pop train production, i.e., they started and stopped their pop trains in unison (Fig. 2B and Fig. S3). While multi-male pop production is frequent, we only used examples where we were able to localise the start and end of each pop train for each participating male. Figure S3 shows the multi-male pop trains where the percentage overlap of pop trains averaged 83% (range: 76-86%). A randomised time shift analysis revealed that

314 the percentage overlap for all three dyads was significantly higher ($P < 0.05$) than expected if
315 the males were vocalising independently of one another (percentage overlap at chance levels
316 averaged 51%; Fig. S3). As the time shift analysis was concentrated over the multi-pop train
317 sequence, a high percentage overlap was expected to occur by chance levels. Notably, the
318 observed percentage overlaps significantly exceeded this value. These sequences contained 4-
319 7 pop trains and averaged 6.3 s in length (range: 5.5-7.3 s).
320
321 Finally, acoustic coordination between allied males was not restricted to particular alliances
322 or areas. A list of all the second-order alliances occurring in both the eastern and western
323 gulfs of Shark Bay where multi-male popping has been recorded is presented in the
324 Supplementary Information (Table S1).
325
326
327

Discussion

We show that multi-level dolphin alliances perform acoustic coordination in a cooperative context. While allied males frequently engage in synchronous physical behaviour when working together to coerce single oestrus females [31–33], we illustrate here that these males also engage in vocal coordination, whereby males will actively match the production and tempo of their pop vocalisations. Individual male pop trains can vary in a number of attributes, including the number of pops per train, the tempo of popping and the length of inter-train intervals, even within the same pop sequence. Yet multi-male pop trains were generally highly coordinated, with males matching each other's tempo of pop production, even as the tempo changed within the train. Males also coordinated the length and timing of their trains, so that their pop trains overlapped significantly above chance levels. Multi-male pop trains were recorded in second-order alliances across our entire study area in both the eastern and western gulfs of Shark Bay. Given the distance between the gulfs relative to dolphin home range sizes [44] and that both sexes are philopatric [45], acoustic coordination may thus be customary in this population and not a behavioural strategy limited to a select number of alliances.

Intervals between pops produced by each individual within localised multi-male pop exchanges averaged 100 ms (Fig. 3), revealing that tempo matching between males can be strikingly precise, given the rate at which these pops are produced ($\bar{x}$ = 10 pops per s, approx. 600 beats per min (BPM)). Humans can quickly and precisely synchronise to an external beat at 67 – 200 BPM [46,47], and a sulphur-crested cockatoo was capable of synchronisation at around 100 BPM [48], both notably slower than the 600 BPM we report here. However, studies on both these species tested their capacity for rhythmic entrainment with a metronome, where motor synchrony, such as tapping a finger or bobbing a head, occurred at a

354 phase offset of 0° (i.e., behaviour occurs at the same time as the beat). In our study, males did
355 not always overlap individual pops, nor did we quantify phase offset, thus we did not find
356 evidence of acoustic synchrony i.e., the precise coincidence of pops in time. In fact, if the
357 signal to the female is based on presenting a unified front of two cooperating males, it is
358 possible that males avoid more precise phase locking of individual pops to prevent masking.
359 However, males did match pop train production where trains significantly overlapped. Given
360 that the pops are rarely, if ever, produced on their own and the vocal unit appears to be the
361 pop train, we suggest that synchrony may be occurring at the level of the pop train.
362
363 It is possible that the males are being entrained by some unknown factor rather than actively
364 coordinating with each another. However, poor underwater visibility in Shark Bay would
365 make vocal entrainment on a physical signal extremely challenging, and no other acoustic
366 signal was found to be associated with multi-male pop production, so we deem this highly
367 unlikely. The bottlenose dolphin's vocal flexibility and propensity for synchronising their
368 movement with social partners [31,32] suggest that they should be able to synchronise
369 auditory output. Given that the range of individual inter-pop intervals over which males can
370 make tempo adjustments in localised multi-male trains (43-173 ms), is similar to the range of
371 values found for dolphin motor synchrony (77-150 ms [32]), this species seems capable of
372 coordination across modalities. To address this with greater certainty, playback experiments
373 could be used to determine how readily individuals adjust their pop production to coordinate
374 with a simulated popping male, and whether they are capable of precise acoustic synchrony.
375
376 It has previously been hypothesised that human pulse perception and entrainment evolved as
377 a result of sexual selection, i.e., multi-male vocal displays helped attract migrating females
378 [17,49,50]. Recently, however, it was shown that males and females are comparable in their

379 vocal entrainment abilities [17,50], and thus a more favourable hypothesis is that the human
380 capacity to perceive and synchronise with rhythms evolved to facilitate cooperative social
381 interactions [17,50]. Indeed, cooperation is wide-spread in human societies and synchrony is
382 an effective mechanism for promoting cooperation by strengthening social attachment among
383 group members [15]. We show that both motor synchrony and acoustic coordination play an
384 important role in the cooperative interactions between male dolphins in Shark Bay
385 [31,32,39]. In the context of consortships, allied male dolphins work together to herd a
386 female and defend her from rival alliances, yet they are also competing for a resource that is
387 indivisible (fertilisation).
388
389 It has been suggested that alliance synchrony during consortships might reduce tension
390 between males in a context that requires them to cooperate successfully [32]. The mechanism
391 underlying this relationship may be hormonal, as studies have linked synchronous behaviour
392 to the release of the neuropeptide oxytocin in humans, which promotes trust and cooperation
393 [51,52] and improves social communication [53]. While a link between synchrony and
394 oxytocin release is yet to be demonstrated in dolphins, a link between oxytocin and prosocial
395 behaviour has been demonstrated in other non-human animals, such as meerkats [54],
396 chimpanzees [55] and grey seals [56] (reviewed in [57]). A positive feedback system may
397 therefore exist between oxytocin release and coordinated behaviour, which would not only
398 promote in-group trust and cooperation but also help regulate stress between allied males in
399 competitive contexts (e.g., consortships). Instances of synchronous behaviour in other taxa
400 and the selective pressures driving their evolution are important to consider when interpreting
401 the motivation behind coordinated displays. Coordinated displays appear to play an important
402 role in promoting cooperative partnerships in human societies [1,15,17]. Our work suggests
403 that acoustic coordination in dolphins also promotes cooperative behaviour, providing further

evidence that coordination, in both motor and acoustic forms, can be a collective feature of cooperation that enhances inclusive fitness by facilitating joint action tasks.

Ethics

Permits for the scientific use of animals were obtained from the Department of Biodiversity, Conservation and Attractions (DBCA), Western Australia. The University of Western Australia, University of Zürich and University of Bristol granted animal ethics approvals.

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Data Accessibility

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.r2280gb9h

Author Contributions

B.L.M. and S.L.K. conceived study; S.L.K., R.C.C. and M.K. acquired funding; S.L.K., B.L.M., S.J.A., R.C.C. and M.K. collected data; B.L.M. and S.L.K. conducted analysis and drafted manuscript; all authors edited manuscript and approved submission.

References

1. McNeill WM. 1995 *Keeping together in time: dance and drill in human history*. Cambridge, MA: Harvard University Press.
2. Backwell PRY. 2018 Synchronous waving in fiddler crabs: a review. *Curr. Zool.* **65**, 83–88. (doi:10.1093/cz/zoy053)
3. Buck J. 1988 Synchronous Rhythmic Flashing of Fireflies II. *Q. Rev. Biol.* **63**, 265–289.
4. Buck J. 1938 Synchronous Rhythmic Flashing of Fireflies. *Q. Rev. Biol.* **13**, 301–314. (doi:10.1086/516403)
5. Greenfield M. 1994 Synchronous and alternating choruses in insects and anurans: common mechanisms and diverse functions. *Am. Zool.* **34**, 605–615.
6. Greenfield MD, Roizen I. 1993 Katydid synchronous chorusing is an evolutionarily stable outcome of female choice. *Nature* , 618–620.
7. Ravignani A. 2017 Agree on definitions of synchrony. *Nature* **545**, 158.
8. Ravignani A, Verga L, Greenfield MD. 2019 Interactive rhythms across species: the evolutionary biology of animal chorusing and turn-taking. *Ann. N. Y. Acad. Sci.* **1453**, 12–21. (doi:10.1111/nyas.14230)
9. Hartbauer M, Römer H. 2016 Rhythm generation and rhythm perception in insects: The evolution of synchronous choruses. *Front. Neurosci.* **10**, 1–15. (doi:10.3389/fnins.2016.00223)
10. Fessler DMT, Holbrook C. 2014 Marching into battle: Synchronized walking diminishes the conceptualized formidability of an antagonist in men. *Biol. Lett.* **10**. (doi:10.1098/rsbl.2014.0592)
11. Launay J, Tarr B, Dunbar RIM. 2016 Synchrony as an adaptive mechanism for large-scale human social bonding. *Ethology* **122**, 779–789. (doi:10.1111/eth.12528)
12. Tarr B, Launay J, Cohen E, Dunbar R. 2015 Synchrony and exertion during dance independently raise pain threshold and encourage social bonding. *Biol. Lett.* **11**, 1–4. (doi:10.1098/rsbl.2015.0767)
13. Reddish P, Fischer R, Bulbulia J. 2013 Let's Dance Together: Synchrony, Shared Intentionality and Cooperation. *PLoS One* **8**. (doi:10.1371/journal.pone.0071182)
14. Valdesolo P, Ouyang J, DeSteno D. 2010 The rhythm of joint action: Synchrony promotes cooperative ability. *J. Exp. Soc. Psychol.* **46**, 693–695. (doi:10.1016/j.jesp.2010.03.004)
15. Wiltermuth SS, Heath C. 2008 Synchrony and Cooperation. *Psychol. Sci.* **20(1)**, 1–5.
16. von Zimmermann J, Richardson DC. 2016 Verbal synchrony and action dynamics in large groups. *Front. Psychol.* **7**, 1–10. (doi:10.3389/fpsyg.2016.02034)
17. Ravignani A, Bowling DL, Fitch WT. 2014 Chorusing, synchrony, and the evolutionary functions of rhythm. *Front. Psychol.* **5**, 1–15. (doi:10.3389/fpsyg.2014.01118)
18. Geissmann T. 2002 Duet-splitting and the evolution of gibbon songs. *Biol. Rev. Camb. Philos. Soc.* **77**, 57–76. (doi:10.1017/S1464793101005826)
19. Méndez-Cárdenas MG, Zimmermann E. 2009 Duetting - A mechanism to strengthen pair bonds in a dispersed pair-living primate (*Lepilemur edwardsi*)? *Am. J. Phys. Anthropol.* **139**, 523–532. (doi:10.1002/ajpa.21017)
20. Brumm H, Slater P. 2007 Animal Communication: Timing Counts. *Curr. Biol.* **17**, 521–523. (doi:10.1016/j.cub.2007.04.053)
21. Mann NI, Dingess KA, Slater PJB. 2006 Antiphonal four-part synchronized chorusing

478 in a Neotropical wren. *Biol. Lett.* **2**, 1–4. (doi:10.1098/rsbl.2005.0373)
479 22. Hall ML, Peters A. 2008 Coordination between the sexes for territorial defence in a
480 duetting fairy-wren. *Anim. Behav.* **76**, 65–73. (doi:10.1016/j.anbehav.2008.01.010)
481 23. Hall ML. 2004 A review of hypotheses for the functions of avian duetting. *Behav.*
482 *Ecol. Sociobiol.* **55**, 415–430.
483 24. Hall ML, Magrath RD. 2007 Temporal coordination signals coalition quality. *Curr.*
484 *Biol.* **17**, 406–407. (doi:10.1016/j.cub.2007.04.022)
485 25. Levinson SC. 2016 Turn-taking in Human Communication - Origins and Implications
486 for Language Processing. *Trends Cogn. Sci.* **20**, 6–14. (doi:10.1016/j.tics.2015.10.010)
487 26. Demartsev V, Strandburg-Peshkin A, Ruffner M, Manser M. 2018 Vocal Turn-Taking
488 in Meerkat Group Calling Sessions. *Curr. Biol.* **0**, 1–6.
489 (doi:10.1016/j.cub.2018.09.065)
490 27. Takahashi DY, Narayanan DZ, Ghazanfar AA. 2013 Coupled Oscillator Dynamics of
491 Vocal Turn-Taking in Monkeys. *Curr. Biol.* **23**, 2162–2168.
492 (doi:10.1016/j.cub.2013.09.005)
493 28. Allen SJ, Bryant KA, Kraus RHS, Loneragan NR, Kopps AM, Brown AM, Gerber L,
494 Krützen M. 2016 Genetic isolation between coastal and fishery-impacted, offshore
495 bottlenose dolphin (Tursiops spp.) populations. *Mol. Ecol.* **25**, 2735–2753.
496 (doi:10.1111/mec.13622)
497 29. Connor RC, Krützen M. 2015 Male dolphin alliances in Shark Bay: Changing
498 perspectives in a 30-year study. *Anim. Behav.* **103**, 223–235.
499 (doi:10.1016/j.anbehav.2015.02.019)
500 30. Connor RC, Smolker RA, Richards AF. 1992 Two levels of alliance formation among
501 male bottlenose dolphins (*Tursiops sp.*). *Proc. Natl. Acad. Sci. U. S. A.* **89**, 987–990.
502 31. Connor RC. 2007 Dolphin social intelligence: complex alliance relationships in
503 bottlenose dolphins and a consideration of selective environments for extreme brain
504 size evolution in mammals. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **362**, 587–602.
505 (doi:10.1098/rstb.2006.1997)
506 32. Connor RC, Smolker R, Bejder L. 2006 Synchrony, social behaviour and alliance
507 affiliation in Indian Ocean bottlenose dolphins, *Tursiops truncatus*. *Anim. Behav.* **72**,
508 1371–1378.
509 33. McCue LM, Cioffi WR, Heithaus MR, Barrè L, Connor RC. 2011 Synchrony,
510 leadership, and association in male Indo-pacific bottlenose dolphins (Tursiops
511 aduncus). *Ethology* (doi:10.1016/j.optmat.2011.11.002)
512 34. Connor RC, Smolker RA, Richards AF. 1992 Dolphin alliances and coalitions. In
513 *Coalitions and alliances in humans and other animals*, pp. 415–443. Oxford: Oxford
514 University Press.
515 35. Connor RC, Smolker RA. 1996 ‘Pop’’ goes the dolphin: a vocalization male
516 bottlenose dolphins produce during consortships.’ *Behaviour* **133**, 643–662.
517 36. Vollmer NL, Hayek LC, Heithaus MR, Connor RC. 2015 Further evidence of a
518 context-specific agonistic signal in bottlenose dolphins: the influence of consortships
519 and group size on the pop vocalization. *Behaviour* **152**, 1979–2000.
520 37. King S, Allen S, Krützen M, Connor R. 2019 Vocal behaviour of allied male dolphins
521 during cooperative mate guarding. *Anim. Cogn.* (doi:https://doi.org/10.1007/s10071-
522 019-01290-1)
523 38. Smolker RA, Richards AF, Connor RC, Pepper JW. 1992 Sex differences in patterns
524 of association among indian ocean bottlenose dolphins. *Behaviour* **123**, 38–69.
525 39. King SL, Friedman WF, Allen SJ, Gerber L, Jensen FH, Wittwer S, Connor RC,
526 Krutzen M. 2018 Bottlenose dolphins retain individual vocal labels in multi-level
527 alliances. *Curr. Biol.* **28**, 1993–1999. (doi:https:// doi.org/10.1016/j.cub.2018.05.013)

40. Gerber L, Connor RC, King SL, Allen SJ, Wittwer S, Bizzozzero MR, Friedman WR, Kalberer S, Sherwin WB. 2019 Affiliation history and age similarity predict alliance formation in adult male bottlenose dolphins. *Behav. Ecol.* , 1–10. (doi:10.1093/beheco/arz195)
41. Quick NJ, Rendell LE, Janik VM. 2008 A mobile acoustic localisation system for the study of free-ranging dolphins during focal follows. *Mar. Mammal Sci.* **24**, 979–989.
42. Wahlberg M, Møhl B, Madsen PT. 2001 Estimating source position accuracy of a large-aperture hydrophone array for bioacoustics. *J. Acoust. Soc. Am.* **109**, 397–406. (doi:10.1121/1.1329619)
43. Schulz TM, Rendell LE, Whitehead H. 2006 A remotely-piloted acoustic array for studying sperm whale vocal behavior. *Can. Acoust.* **34**, 54–55.
44. Randić S, Connor RC, Sherwin WB, Krützen M. 2012 A novel mammalian social structure in Indo-Pacific bottlenose dolphins (Tursiops sp.): complex male alliances in an open social network. *Proc. Biol. Sci.* **279**, 3083–3090. (doi:10.1098/rspb.2012.0264)
45. Krutzen M, Sherwin WB, Berggren P, Gales N. 2004 Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: Bottlenose dolphins in Shark Bay,Western Australia. *Mar. Mammal Sci.* **20**, 28–47.
46. Repp B. 2013 Sensorimotor synchronization: a review of the tapping literature. *Psychon. Bull. Rev.* **12**, 969–992.
47. Patel AD. 2014 The Evolutionary Biology of Musical Rhythm: Was Darwin Wrong ? *PLoS Biol.* **12**, 1–6. (doi:10.1371/journal.pbio.1001821)
48. Patel AS, Iversen JR, Bregman MR. 2009 Experimental evidence for synchronization to a musical beat in a nonhuman animal. *Curr. Biol.* **19**, 827–830. (doi:10.1016/j.cub.2009.03.038)
49. Merker B. 2000 Synchronous chorusing and the origins of music. *Music. Sci.* **3**, 59–73.
50. Bowling DL, Herbst CT, Fitch WT. 2013 Social origins of rhythm? Synchrony and temporal regularity in human vocalization. *PLoS One* **8**. (doi:10.1371/journal.pone.0080402)
51. De Dreu CKW, Greer LL, Van Kleef GA, Shalvi S, Handgraaf MJJ. 2011 Oxytocin promotes human ethnocentrism. *Proc. Natl. Acad. Sci.* **108**, 1262–1266. (doi:10.1073/pnas.1015316108)
52. De Dreu CKW, Greer LL, Handgraaf MJJ, Shalvi S, Van Kleef GA, Baas M, Ten Velden FS, Van Dijk E, Feith SWW. 2010 The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science (80-.).* **328**, 1408–1411. (doi:10.1126/science.1189047)
53. Spengler FB, Scheele D, Marsh N, Kofferath C, Flach A, Schwarz S, Stoffel-Wagner B, Maier W, Hurlemann R. 2017 Oxytocin facilitates reciprocity in social communication. *Soc. Cogn. Affect. Neurosci.* **12**, 1325–1333. (doi:10.1093/scan/nsx061)
54. Madden JR, Clutton-Brock TH. 2011 Experimental peripheral administration of oxytocin elevates a suite of cooperative behaviours in a wild social mammal. *Proc. R. Soc. B Biol. Sci.* **278**, 1189–1194. (doi:10.1098/rspb.2010.1675)
55. Crockford C, Wittig RM, Langergraber K, Ziegler TE, Zuberbuhler K, Deschner T. 2013 Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B Biol. Sci.* **280**, 20122765. (doi:10.1098/rspb.2012.2765)
56. Robinson KJ, Twiss SD, Hazon N, Moss S, Pomeroy PP. 2017 Positive social behaviours are induced and retained after oxytocin manipulations mimicking endogenous concentrations in a wild mammal. *Proc. R. Soc. B Biol. Sci.* **284**, 20170554. (doi:10.1098/rspb.2017.0554)

57. Crockford C, Deschner T, Ziegler TE, Wittig RM. 2014 Endogenous peripheral oxytocin measures can give insight into the dynamics of social relationships: a review. *Front. Behav. Neurosci.* **8**, 1–14. (doi:10.3389/fnbeh.2014.00068)

Figure Legends

Figure 1. Spectrograms of individual and multi-male pop trains from one second-order alliance (down-sampled to 48 kHz, FFT length: 1024, Hamming window function). (A) Individual male pop trains. (B) Multi-male pop trains.

Figure 2. Localised multi-male pop trains from two different second-order alliances. Spectrogram of multi-male pop trains; (A) sampled at 48 kHz, FFT length: 1024, Hamming window function and (B) down-sampled to 48 kHz, FFT length: 1024, Hamming window function). Both panels show pops produced by two different males (A in white and B in yellow) from two different second-order alliances, and the localised bearing of each pop in relation to the research vessel (0° is the research vessel's bow). Each localised pop is also identified with a coloured dot (corresponding to male A or B) at the base of the pop.

Figure 3. Variation in individual male pop trains. (A) Density plot of the slopes from the linear regression of 279 single male pop trains (total of 2692 pops) recorded from 7 different second-order alliances (one value not visible in density plot, x = 0.028); (B) smoothed linear change in inter-pop-interval (IPI) over time in a subset of localised pop trains produced by six individual males from four different second-order alliances.

Figure 4. Analysis of individual pop tempo when produced in multi-male pop trains. (A) inter-pop interval of male A (n=96) against the inter-pop interval of male B immediately following male A (n=96), across multiple pop trains in the same pop sequence, with corresponding Pearson correlation coefficient; colour-coded by second-order alliance membership (green = RR alliance, grey = KS alliance, red = AC alliance, blue = SB alliance, yellow = PB alliance). Note, this figure does not represent the change in IPI over time but the correlation of consecutive IPIs between male dyads. (B) null model of the expected correlation coefficients based on 1000 permutations of a pop train produced in a multi-male pop train with a pop train produced by a single male (matched for number of pops). The dotted line indicates the observed correlation coefficient, with plots colour-coded by second-order alliance membership. Note, given the lack of correlation for the AC alliance, no null model was created.